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Breeding in a den of thieves: pros and cons of nesting close to egg predators

JIMMY DE FOUW,^{1,2,†} ROELAND A. BOM,^{1,2} RAYMOND H. G. KLAASSEN,^{3,4} GERARD J. D. M. MÜSKENS,⁵ PETER P. DE VRIES,¹ IGOR YU. POPOV,⁶ YAKOV I. KOKOREV,⁷ BARWOLT S. EBBINGE,⁵ AND BART A. NOLET^{1,8}

¹Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), P.O. Box 50, Wageningen, 6700 AB The Netherlands

²Department of Coastal systems, NIOZ Royal Netherlands Institute for Sea Research and Utrecht University, P.O. Box 59, Den Burg (Texel), 1790 AB The Netherlands

³Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, P.O. Box 11103, Groningen, 9700 CC The Netherlands

⁴Dutch Montagu's Harrier Foundation, P.O. Box 46, Scheemda, 9679 ZG The Netherlands

⁵Alterra Wageningen-University and Research Centre, P.O. Box 47, Wageningen, 6700 AA The Netherlands

⁶Laboratory of Biogeocenology and Historical Ecology, A.N. Severtsov Institute of Ecology and Evolution (RAS), 33 Leninskij Prospekt, Moscow, 119071 Russia

⁷Extreme North Agricultural Research Institute, Russian Academy of Agricultural Sciences, Komsomolaskaya Street 1, Norilsk, 663302 Russia

⁸Computational Geo-Ecology, Department of Science, Institute for Biodiversity and Ecosystem Dynamics University of Amsterdam, P.O. Box 94248, Amsterdam, 1090 GE The Netherlands

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Abstract. Breeding success of many Arctic-breeding bird populations varies with lemming cycles due to prey switching behavior of generalist predators. Several bird species breed on islands to escape from generalist predators like Arctic fox *Vulpes lagopus*, but little is known about how these species interact. We studied brent geese *Branta bernicla bernicla* that share islands with gulls (*Larus* spec.) in Taimyr, Siberia (Russia). On one hand, gulls are egg predators, which occasionally steal an egg when incubating geese leave the nest for foraging bouts. On the other hand, gulls import marine resources to the islands, enriching the soil with their guano. We considered three hypotheses regarding clutch size of brent geese after partial nest predation. According to the “predator proximity hypothesis”, clutch size is expected to be smallest close to gulls, because of enhanced predator exposure. Conversely, clutch size is expected to be largest close to gulls, because of the supposedly better feeding conditions close to gulls, which might reduce nest recess times of geese and hence egg predation risk (“guano hypothesis”). Furthermore, gulls may defend their nesting territory, and thus nearby goose nests might benefit from this protection against other gulls (“nest association hypothesis”). We mapped goose and gull nests toward the end of the goose incubation period. In accordance with the latter two hypotheses, goose clutch size decreased with distance to the nearest gull nest in all but the lemming peak year. In the lemming peak year, clutch size was consistently high, indicating that partial nest predation was nearly absent. By mapping food quantity and quality, we found that nitrogen availability was indeed higher closer to gull nests, reflecting guanofication. Unlike predicted by the nest association hypothesis, a predation pressure experiment revealed that egg predation rate decreased with distance to the focal gull nests. We therefore propose that higher food availability close to gulls enables female geese to reduce nest recess time, limiting egg predation by gulls.

Key words: *Branta bernicla bernicla*; clutch size; dark-bellied brent goose; guanofication; gulls; lemming cycle; nest association hypothesis; partial nest predation; Taimyr.

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† **E-mail:** jimmy.de.fouw@nioz.nl

INTRODUCTION

For birds on the tundra, ground-nesting is about the only option, but ground-nesting birds suffer from high rates of nest predation (Martin 1995). Although nest predation is generally thought to be lower at high latitudes than at lower latitudes (McKinnon et al. 2010), many tundra-nesting birds indeed suffer from nest predation. The intensity of nest predation on the tundra is associated with the abundance of generalist predators like Arctic foxes *Vulpes lagopus*, which in turn is a response, time-lagged or not, to the abundance of rodents, in particular lemmings *Lemmus* spp. and *Dicrostonyx* spp. (Gauthier et al. 2004).

The dark-bellied brent goose (*Branta bernicla bernicla*; hereafter brent goose) is a typical ground-nesting bird of the tundra of Taimyr, Russia. They have three main breeding strategies to deal with nest predation: cryptic breeding, breeding around nesting snowy owls *Bubo scandiacus*, and breeding on islands (Ebbinge and Spaans 2002). Cryptic breeding, i.e. breeding in single pairs spread over the mainland, is a rare but perhaps underestimated strategy. Nesting within breeding territories of snowy owls, also on the mainland, is another strategy. Snowy owls actively defend the direct vicinity of their nest against predators, creating safe territories for breeding geese (Summers et al. 1994) (“nest association hypothesis” (NAH, Bêty et al. 2001)). However, this strategy is only available in years when lemmings (*Lemmus sibiricus* and *Dicrostonyx torquatus*) are abundant (so-called “lemming peak years”), as snowy owls are nomadic (Fuller et al. 2003, Therrien et al. 2014) and only breed when there are sufficient lemmings (their focal prey when nesting). Nesting on small islands is presumably the most common breeding strategy, and in any case available in all years, because these islands are generally free from Arctic foxes (Ebbinge and Spaans 2002, Ebbinge et al. 2002). These islands are also inhabited, probably for the same reason, by other birds, most notably colonies of Taimyr gull (*Larus taimyrensis*) (Liebers et al. 2004).

Previous research on brent geese breeding on offshore islands in the Pyasina Delta, Taimyr, Siberia (Russia), during two complete lemming cycles (1990–1995) revealed that lemming abundance has an important effect on the number and reproduction of geese breeding on islands (Ebbinge 2000).

Larger numbers of geese inhabited the islands in years with fewer lemmings, i.e. when breeding near snowy owls is not an option. In years when lemmings were scarce, clutch size at hatching was on average 0.8 eggs smaller than in years when lemmings were abundant (Ebbinge and Spaans 2002, Ebbinge et al. 2002). The latter was explained by higher predation of eggs by gulls in non-peak years (Ebbinge 2000). In brent geese only the female incubates whereas the male guards the nest (Poisbleau et al. 2007). The female leaves the nest about 13 times a day for 15 min to forage, and gulls typically grab a goose egg during these nest recesses of the female (Spaans et al. 2007). Hence, clutch predation is typically only partial.

Because gulls are egg predators, one might expect clutch size of brent geese to be smallest close to gulls (“predator proximity hypothesis”), as has been found in other goose species (van der Jeugd et al. 2003). However, brent geese often nest within gull colonies and remarkably close to gull nests (Ebbinge and Spaans 2002). Two non-mutually exclusive hypotheses have been put forward to explain this phenomenon, both proposing that nesting close to gulls would reduce egg predation risk, albeit through different mechanisms. According to the first hypothesis, the “nest association hypothesis”, the neighboring gull would defend its nesting territory, thereby providing the nearby goose nest protection against other gulls (Ebbinge and Spaans 2002). Predator protection by symbiotic nesting (reviewed in Haemig 2001), is a common phenomenon among tundra birds (Larsen and Grundetjern 1997, Bêty et al. 2001, Prop and Quinn 2003, Quinn et al. 2003, Quinn and Ueta 2008). According to the second hypothesis, the “guano hypothesis”, the soil near gull nests is enriched with their guano (Sanchez-Pinero and Polis 2000), offering better feeding conditions to the geese, which might enable them to stay close to the nest and reduce nest recess duration, and hence egg predation risk (Ebbinge and Spaans 2002, Spaans et al. 2007).

In this article, we test whether brent goose clutch size decreases or increases with distance to gull nests, and whether this effect varies with lemming abundance. For this purpose, we use a large data set on goose and gull clutch size and positions, on nine different islands with different densities of nesting gulls, collected during five years (i.e. covering one whole lemming cycle). Furthermore, we test two predictions derived

from our two main hypotheses (“nest association hypothesis” and “guano hypothesis”) on one of the islands in one year when nearly all geese had abandoned their nests prematurely after a fox had visited the island during the incubation phase.

In order to test the prediction of the “nest association hypothesis”, that egg predation risk was lower close to gull nests, we conducted an egg predation experiment using artificial goose nests. This approach using artificial nests has been used successfully in other studies of predation risk in the Arctic (McKinnon et al. 2010, 2013). In order to test the prediction of the “guano hypothesis”, that food availability was better close to gull nests, we mapped goose food quality and quantity. We combined food quality and quantity in one measure (gram nitrogen per m²), while taking differences in nitrogen availability to herbivores between monocot and dicot plants into account (DeGabriel et al. 2008).

METHODS

Study area

Dark-bellied Brent geese breed in remote areas, in the coastal zone of northern Siberia (Russia), stretching from the Yamal peninsula to the eastern shores of the Taimyr peninsula (Ebbinge et al. 1999). Our study was conducted on islands in western Taimyr (Fig. 1), at the mouth of the Pyasina river, Russia (74°07' N, 86°50' E) in five years (2004–2008). In Taimyr, lemming cycles

typically last three years (Kokorev and Kuksov 2002), with some irregularity in recent years (Nolet et al. 2013). The majority of brent geese breed on islands which consist of rocks and tundra vegetation, and on rocky islands with bare and tundra patches, both types of islands having a more grassy vegetation around colonies of gulls (Spaans et al. 2007). In most years, the islands off the coast of Taimyr are free from the main egg predator on the mainland tundra, the Arctic fox, which is only able to visit these islands during the goose breeding season in years with exceptionally late sea ice cover (Spaans et al. 1998). In 2008, a late spring, virtually all brent goose nests were depredated due to an Arctic fox visiting most islands over the ice in the beginning of the incubation period. We used this opportunity to map nitrogen availability, and perform an egg predation risk experiment on one of the larger (15.3 ha) islands, which became our focal study island (Big Bird Island, BBI) (Spaans et al. 2007).

Island surveys

Twelve islands were visited by us, of which seven each year. Brent geese are highly susceptible to disturbance, making it difficult to take samples on the islands during the goose incubation phase. Each year a nest survey was done in the third week of incubation by brent geese, and hence the determined clutch size reflects the initial clutch size minus eggs depredated up to that moment.

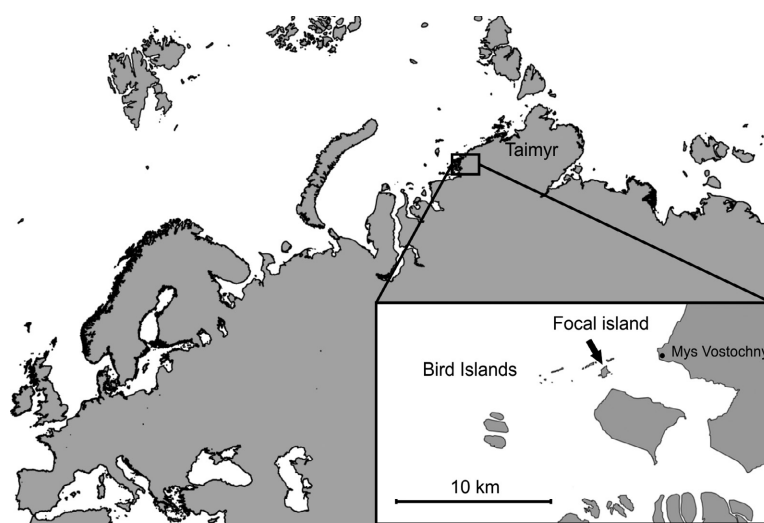


Fig. 1. Study area at the Pyasina Delta on the Taimyr Peninsula in northern Siberia, Russia.

The nest survey was always done as quickly as possible in order to limit egg predation by gulls during the survey. Nests of geese and gulls, both active and abandoned or depredated, were mapped with handheld GPS-devices (Garmin 12, Garmin 76, Garmin eTrek, accuracy on open tundra and device operational during whole survey: 3–5 m). After egg hatching, the islands were searched again in order to check for missed nests. Clutch size was predicted using a generalized linear mixed model with Poisson distribution (function *glmer*, package *Lme4* in R Development Core Team 2014), with continuous variable distance to the nearest gull nest, and year as a fixed factor and island as a random factor. The Poisson distribution of clutch size contained zeroes, potentially leading to overdispersion, but this was not detected (ratio between residual deviance and residual degrees of freedom: $\hat{c} = 0.96 \approx 1$). Variance inflation factors (VIF) of the fixed effects were computed and there was no multicollinearity detected (VIF <1.1). Models were ranked according Akaike's Information Criterion (AIC; Burnham and Anderson 2002). Models of which the AIC differed more than 2 from the most parsimonious model were considered to have no substantial empirical support (Burnham and Anderson 2002).

Focal study island

On 7 July 2008, we noted an Arctic fox depredating brent geese nests at Big Bird Island. The fox managed to discover all brent geese nests except two, and we recorded it collecting 79 eggs, three of which were eaten and 76 were buried. Following this major predation event, the island was nearly void of nesting brent geese, providing a unique opportunity to visit the island intensively during the breeding season for other purposes than a quick nest inventory.

Egg predation experiment

We measured egg predation rate in relation to the distance to a gull's nest by putting out artificial nests on 16–19 July 2008, and recording the duration until predation by a gull. In this way, predation rate could be tested independently from the quality of individual brent geese. Goose down of depredated nests was used to create artificial nests that mimic the situation when the female is foraging away from

the nest, accompanied by the male (Fig. 2). Artificial nests were placed along a line transect at 5, 15, 25, 35, 45, 55, 65 and 75 m from the nest of the nearest gull nesting at the edge of the colony (to make sure no gull was nesting closer than the assigned distances). The artificial nests were marked with small wooden sticks at 1 m distance. Two observers watched the artificial nests from a hide (c. 4 m high). Three assistants lined up along the transect, and at a call by the observers through radio contact, quickly placed one chicken egg in each nest, and partly covered up with goose down (Fig. 2a). Only after all eight nests had received their egg, the assistants simultaneously retreated, and the trial started. The two observers noted for each nest the time until predation of the egg by a gull occurred. If not all nest were depredated after 1 h the whole transect was walked and checked; this was repeated once every hour. Trials were performed at four parts of the gull colonies along the coastline, and these four trials were replicated, starting from a different gull's nest (Fig. 3a). Time to predation, log-transformed to obtain normality, was fitted using a linear mixed-effects model, with colony part and replicate as random factors (replicate nested in colony part) (function *lme*, package *nlme* in R Development Core Team 2014).

Mapping food quality and quantity

Aboveground plant material was sampled on a grid on 16–20 July 2008. Sampling points were 50 m apart, with additional sampling points located at the edges of the island in the east-west direction (total $n = 72$) (Fig. 3b). All aboveground plant material was clipped within rings with an inner surface of 0.08 m² (or 0.15 m² when vegetation was sparse, $n = 8$). Within two days, the samples were sorted, and all potential brent goose food plants collected. In order to correct for differences in nitrogen availability, we distinguished between monocots (grasses *Eriophorum angustifolium* and *Poa arctica*, and sedges *Carex bigelowii*) and dicots (willows *Salix polaris* and *S. reptans*). All collected material was dried above a wood stove, and transported for further analysis. Biomass of monocots and dicots was measured to the nearest 0.1 mg. Of each sample, a subsample was taken to measure the mass proportion of N and C with a Euro EA 3000 elemental

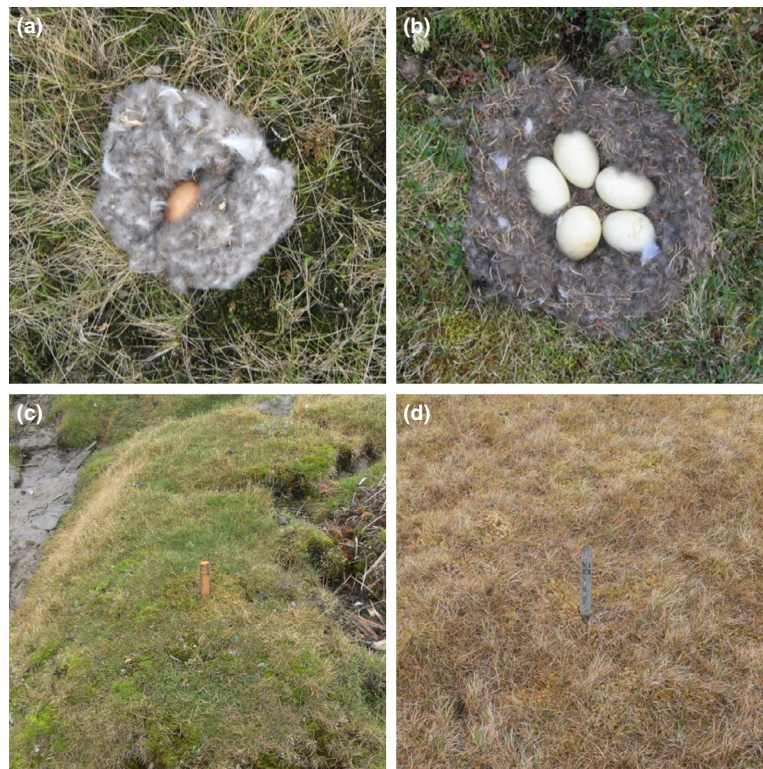


Fig. 2. Created artificial nests with goose down of predated nests (a). Natural goose nest on one of the islands (b). Tundra vegetation within and close to a gull colony (c). Tundra vegetation in the middle of the island outside gull colony (d).

analyzer (Eurovector, Milan, Italy), coupled through a Finnigan con-flo interface to a Finnigan Delta S isotope ratio mass spectrometry (Thermo Scientific, Bremen, Germany). This analysis is based on the Pregl-Dumas technique. Mass percentage N and C of the standard acetanilide yielded $10.36\% \pm 0.02$ and $71.16\% \pm 0.20$, respectively (mean \pm SD, $n = 11$). Tannins can bind nitrogen, and we used a method developed by DeGabriel et al. (2008) to correct for this by measuring the polyethylene glycol (PEG) binding capacity in mixtures of monocots ($n = 2$) and dicots ($n = 6$). This yields the fraction available N per monocot or dicot part of the sample. For monocots and dicots separately, total available nitrogen (gN m^{-2}) was obtained by multiplying the biomass (g m^{-2}) by the mass proportion of N and the fraction available N. Finally, total available nitrogen (gN m^{-2}) was obtained by summing the totals of monocots and dicots per sampling point. The sampling points were photographed on 21 July 2008, and the greenness

scored on a scale ranging from 1 to 10 (Fig. 2c,d). Biomass data of two sample points on the grid were missing, and available gN m^{-2} was estimated from greenness based on the regression of the available gN m^{-2} on the greenness index of the other sampling points ($R^2 = 0.73$). Nitrogen was predicted using a linear model with distance to the first gull nest as exploratory variable. Analyses were executed in (R Development Core Team 2014).

Lemming abundance

During summer (end June–mid August) lemmings were caught in snap-traps along a transect in different tundra habitats on the adjacent mainland (Mys Vostochny) (Fig. 1) (Rykhlikova and Popov 2000). The main species is the Siberian lemming *L. sibiricus* and less abundant was the collared lemming *D. torquatus* (Nolet et al. 2013). Relative lemming abundance was calculated by the total number of lemmings caught per 100 trap-days.

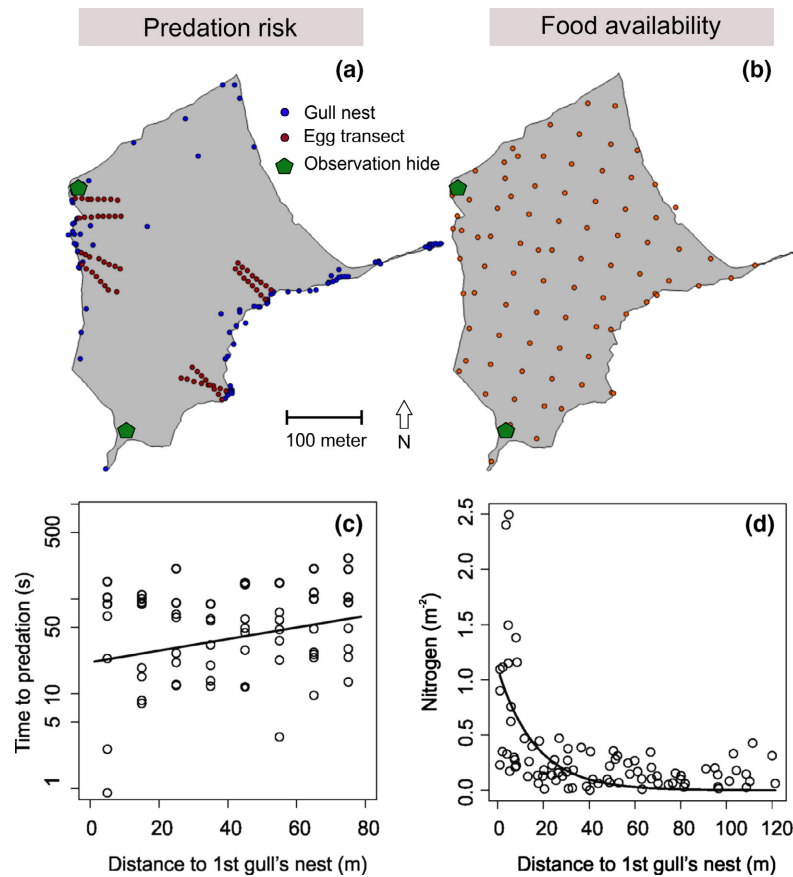


Fig. 3. Location of artificial nests along transects in the egg predation experiment in relation to nests of gull (a). Time to predation was observed from the observation hides. Grid to sample available nitrogen (b). Time to predation of egg in artificial nests located along transects away from the gull's colony (c). Non-linear relationship between available nitrogen per m^2 and distance to the first gull nest (d).

RESULTS

Annual variation in geese, gulls and lemmings

In 2005 we observed a lemming peak-year and in other years lemming numbers were very low or absent (Fig. 4). At the seven islands that were checked each year, the total number of brent goose nests differed notably among years: 257, 143, 106, 217 and 121 nests in 2004 till 2008, respectively (Appendix S1). There was no temporal trend in number of nests (Pearson's $R = -0.48$, $n = 5$, $P = 0.42$). Average clutch size of brent geese ranged from $0.48 (\pm 0.01)$ in 2008 to $3.14 (\pm 0.10)$ in 2005 for the lemming peak year. Among years, numbers of gull nests also varied, showing a significant negative trend (2004–2008): 1123, 1224, 984, 769, and 717 gull

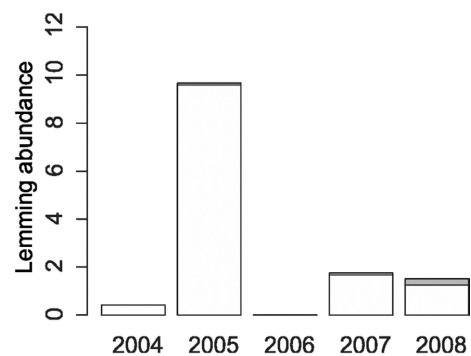


Fig. 4. Lemming abundance during summer of 2004–2008 (end June–mid August) in our study area in total number of lemmings caught per 100 trap-days. The main species is the Siberian lemming *Lemmus sibiricus* (white) and less abundant was the collared lemming *Dicrostonyx torquatus* (grey).

Table 1. The explanatory models of dark-bellied brent goose clutch size at nine islands in the Pyasina Delta according to Akaike's information criterion (Burnham and Anderson 2002). Independent variables: distance to the first gull (dis1stgull) and year and island as a random factor. K is the number of parameters, ω_i is its Akaike's weight (Burnham and Anderson 2002).

Model	Clutch size	K	ΔAIC	ω_i
1	Year + dis1 st gull + year \times dis1 st gull	11	0	1.00
2	Year + dis1 st gull	7	92.52	0.00
3	Year	6	100.87	0.00
4	dis1 st gull	3	361.79	0.00

nests respectively (Pearson's $R = -0.91$, $n = 5$, $P < 0.05$).

Island surveys

Based on ΔAIC , the full model with distance to the first gull, year and their interaction was considered the best model to explain brent goose clutch size on the islands (Table 1). For most years there was a negative trend between clutch size and distance to the first gull, but in 2005, the lemming peak year, no negative relation between clutch size and distance to the first gull was found (Fig. 5).

Egg predation experiment

At the start of the experiment, all gulls were in the air, but after 02:55 min \pm 02:14 min (mean \pm SD) they had returned to their nest to incubate. Gulls were very quiet during incubation. Occasionally a flying gull discovered an artificial nest, and sometimes depredated it. If so, other nearby gulls were always reacting by chasing the gull in an attempt to steal the discovered food, sometimes resulting in discovery and depredation of other artificial nests. Time to predation was positively related to the distance to the first gull nest, with the artificial nests closest to the nearest gull nest suffering the highest egg predation rate ($t_{55} = 3.19$, $P = 0.0023$; Table 2; Fig. 3c). Instead of protecting the neighboring goose nest, an incubating gull sometimes depredated this nearest artificial nest.

Food quality and quantity

The binding effect of PEG for monocots was 0.96 (SD \pm 0.001) and for dicots 0.76 (SD \pm

0.058), respectively, indicating that nearly all nitrogen in monocots was available to the herbivore, whereas c. 24% was not in dicots. Nitrogen availability decreased non-linearly with distance to the first gull nest ($t_{1,91} = -3.89$, $P < 0.001$, Fig. 3d), with higher nitrogen availability within 10 m of the first gull nest.

DISCUSSION

Overall, in contrast with the "predator proximity hypothesis", we found a larger clutch size in island-breeding geese when nesting nearer to gull nests. Brent goose clutch size was also affected by year, related to differences among years in the abundance of lemmings. In years when lemmings were scarce, goose clutch size decreased with distance to the nearest nesting gull, whereas in the year when lemmings were abundant (i.e., 2005), there was no such relation (Fig. 5). In that year, clutch size was also generally larger, indicating that goose egg predation was lower in such a lemming peak year. These observations suggest that the decrease in clutch size with distance to the nearest gull nest is caused by partial predation by gulls, and not solely by better quality individual geese nesting close to gulls. It also suggests that lemming abundance has an indirect positive effect on goose egg survival which is caused by prey switching behavior of the gulls (Fig. 6). Indeed, in 2005 when their preferred food (i.e. lemmings) was available to the gulls, lemming remains were frequently found near many gull nests (*personal observation*).

A positive association between goose clutch size and gull presence, at least in years when lemmings are scarce, was hypothesized for both the "nest association hypothesis" and the "guano hypothesis". Thus, the egg predation experiment and the description of nitrogen availability were needed to distinguish between these two alternative ideas. Results of our egg predation experiment did not provide support for the "nest association hypothesis" as we observed that artificial nests close to the nearest gull nests suffered the highest egg predation rate. To avoid confounding effects of other nearby gulls, and to match the scale at which natural patterns in brent geese clutch size were described we chose to measure predation rate in the experiment from the edge of the gull colony outward (i.e., the focal

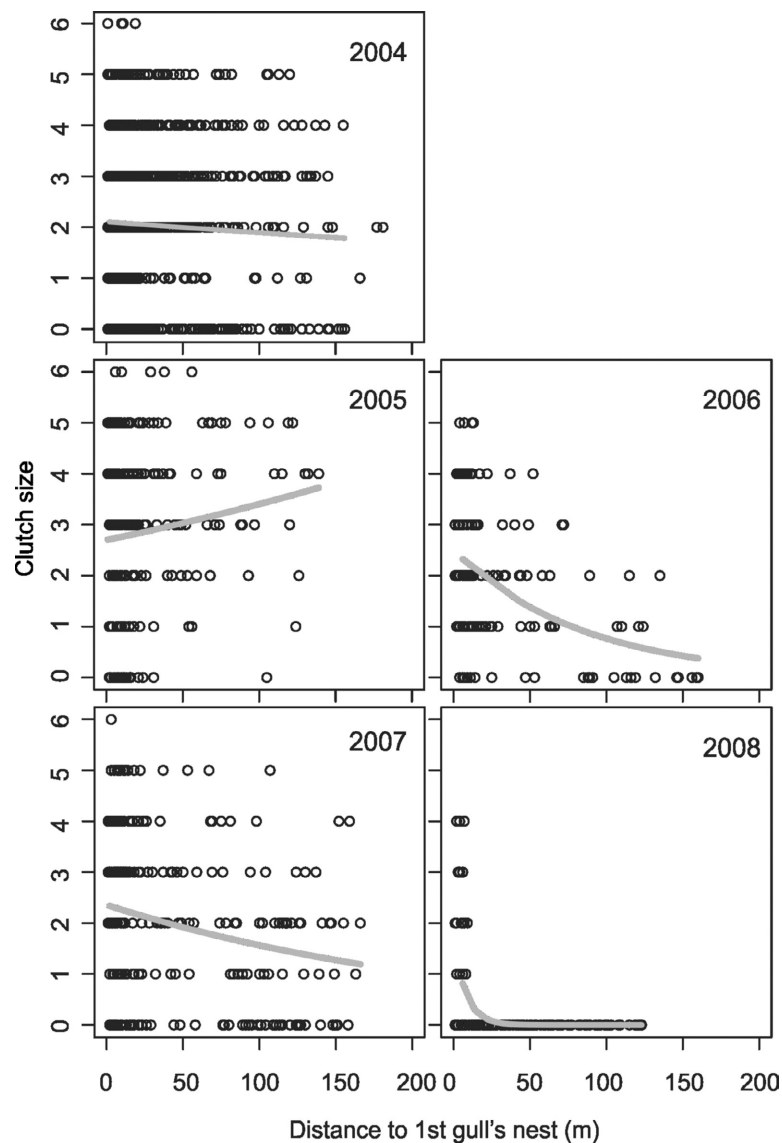


Fig. 5. Goose clutch size as function of distance to the first gull and year. Predicted values (grey line) according to model 1 (see Table 1).

Table 2. Generalized mixed effect model of time to predation. With distance to the first gull as continuous fixed effect and transect and replicate (nested in transect) as random variable.

Effects	Estimate	SE	df	t	P
Fixed					
Intercept	3.19	0.15	55	20.48	<0.01
Dis1 st gull	0.005	0.0016	55	3.19	<0.05
Random					
Transect	SD = 1.96×10^{-5}				
Replicate	SD = 0.39				

gull nest was always also the nearest gull nest). Perhaps results would have been different if we would have compared egg predation rate within and outside gull colonies. This was the approach used in a study of common eiders *Somateria mollissima* nesting on islands also inhabited by various gull species. The results of these experiments depended on the nesting phase of the eiders: in the incubation period there was no significant difference in the survival time of artificial eider nests (Götmark and Åhlund 1988), but earlier,

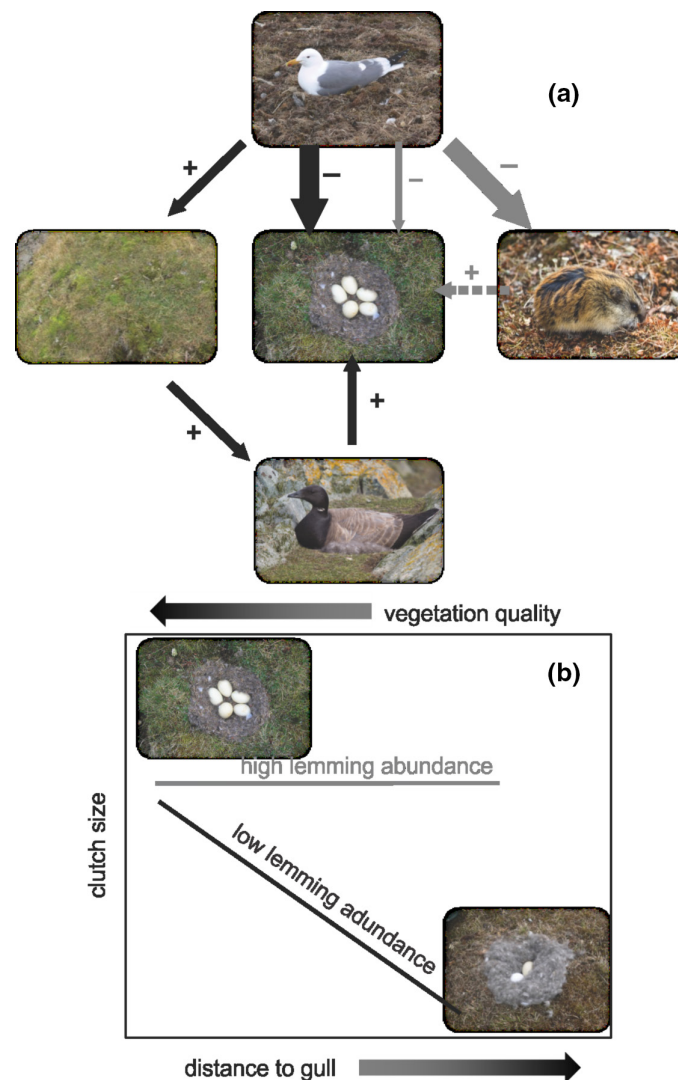


Fig. 6. Conceptual representation of the direct (full arrows) and indirect (stippled arrow) interactions between gulls, brent geese and lemmings on tundra islands during the breeding season (a). The relation between brent geese clutch size and distance to the gull in lemming year (grey line) and in years with low lemming abundance (black line) (b). See main text for explanation. (Photo credit for images of lemming and brent geese: Andries Datema).

in the laying period, when the gulls had no eggs yet, the proportion of depredated artificial nests was higher within than outside the gull colonies (Gotmark 1989), similar to our experimental finding. Also consistent with our findings, in herring gulls *Larus argentatus*, nests closer to the nearest other gull nest had a higher chance of being depredated (Brouwer and Spaans 1994). The same pattern was found for hen harriers *Circus cyaneus*, where fledging success increased with increasing distance from the gull colony

(Schipper 1978). Only Burger (1984) reported that the time to predation was shorter for artificial gull nests located >200 m from gull nests than for those within a herring gull colony, supporting the “nest association hypothesis”. However, in that study, artificial nests were laid out in open grass whereas the percentage bush cover was far more important for the time to predation than the density of gulls (Burger 1984).

Thus, generally, in terms of egg predation risks, nesting geese and ducks seem to be better off fur-

ther away from nesting gulls. These results can be understood in light of the incubation ecology of gulls. Gulls incubate their eggs continuously, since, in contrast with geese, both members of a pair share incubation duties (Tinbergen 1960). Thus, their eggs are mainly protected against other gulls, not by actively chasing other gulls away, but by passively sticking to the nest. During our experimental trials, we indeed never saw an incubating gull chasing other gulls, when deprecating the artificial nest close to its own nest.

The results of our analysis of nitrogen availability in relation to distance to gull nest provided support for the “guano hypothesis”. The available nitrogen within goose nesting territories was higher closer to gulls. This could be explained by enrichment of the vegetation by the guano of the gulls. This potentially offers good feeding conditions to geese within their nesting territories, enabling the females to stay close to the nest and reduce nest recess duration, and hence egg predation risk. Feeding conditions are known to be important in habitat selection, and are among the main resources that constrain populations (Newton 1998). Lesser snow geese *Chen caerulescens caerulescens* that nest in places with better nutrient availability showed a higher clutch size and reproductive success (Cooke et al. 1995). Barnacle geese *Branta leucopsis* had a preference for feeding sites where guano enhanced nitrogen content of the vegetation, both prior to autumn migration near seabird cliffs (Prop et al. 1984) and at wintering grounds within gull nesting sites (Bazely et al. 1991).

We were able to reject the “predator proximity hypothesis” convincingly. However, future research should try and set out to test our two remaining hypotheses in a cross-design, as currently distance to the nearest gull nest is confounded with nitrogen abundance. Such a design would involve creating patches with increased nitrogen availability away from gulls, for instance by adding nutrients in far-away patches, and creating patches with decreased nitrogen availability nearby gulls, for instance by removing vegetation or adding snow (thereby delaying the growth season). In addition, it would be particularly interesting to collect data on nest recess times, in order to arrive at a more mechanistic understanding of egg predation rates: if the “guano hypothesis” is true, we would expect that nest recess time is a negative function of nitrogen availability in

the breeding territory, and, in the natural setting, a positive function of distance to the nearest gull.

As the brent geese population grows (Nolet et al. 2013), breeding on the mainland is expected to become more attractive to brent geese, but apart from small numbers scattered over the tundra (cryptic breeding), this is only possible in lemming years in the vicinity of snowy owl nests (Ebbinge and Spaans 2002). It is interesting that brent geese nesting within territories of snowy owls have on average even larger clutches (4–5 eggs) (Summers et al. 1994, van Kleef et al. 2007) than the highest average clutches observed in brent geese nesting in gull colonies in lemming peak years. However, in lemming peak years, the only years that snowy owls breed, egg predation rate on the islands is lower than in other years. For the time being, breeding near snowy owls seems to be the most preferred strategy, judging from the fact that the number of geese breeding on the islands was lowest in lemming peak years.

Currently, the sustainability of the brent geese population is highly dependent on the reproduction during lemming peak years (Nolet et al. 2013). In Taimyr, our study region, lemming peak years occur since 1994 less regularly and are less massive, in particular in the 2000s (Nolet et al. 2013). There are multiple lines of evidence that in various places in the Arctic, lemming cycles are faltering or even collapsing (Ims et al. 2008). These changes could have large effects on arctic predators like snowy owls, skuas, Arctic foxes (Schmidt et al. 2012) and, possibly, gulls. However, when lemming peak years will become rarer, the overall abundance of generalist predators may eventually fall, and with this the predation pressure in low lemming years. There are indeed indications that, for example, the number of nesting gulls is declining in our study area since 1990 (number of Taimyr gulls vs. year, ANOVA, $F_{1,4} = 13.88$, $P = 0.02$, no significant effect of lemming peak was detected, $F_{1,4} = 4.57$, $P = 0.1$, unpublished data). How these changes will affect the brent goose population and in a broader sense the reproductive success of Arctic-nesting migratory birds is an open question.

Based on our current results we argue that bottom-up effects mediated by vegetation quality are the main driver behind the larger clutches of brent geese found close to gulls. However, at the same time we also found clear indications for top-down effects (Fig. 6). Mean clutch size varied

greatly among years, being strongly positively correlated with lemming abundance, indicating the general importance of egg predation on the reproduction of brent geese (see also Ebbinge and Spaans 2002). Moreover, one could argue that the effect of vegetation (bottom-up regulation) is mediated through egg predation by gulls (top-down regulation), as discussed above. Indeed, in years with high predation (i.e. few lemmings, thus strong top-down effects), the relationship between clutch size and distance to gull was strongest, suggesting that without gull predation, vegetation quality would play less of a role (Fig. 6). Finally, island-breeding by brent geese most likely has evolved in order to avoid predation from mammalian predators in the first place (Quinn et al. 2003). Therefore, both bottom-up and top-down effects are important in shaping brent goose nesting (Gauthier et al. 2004).

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